

SYSTEMATICS, GROWTH, AND DEVELOPMENT OF *LAFOEINA*
MAXIMA(=*KERATOSUM COMPLEXUM*) (HYDROZOA,
CAMPANULINIDAE)

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ABSTRACT

Keratosum complexum Hargitt, 1909, is a junior synonym of *Lafoeina maxima* Levinsen, 1893. Several specimens have been collected from the type locality of *K. complexum* and compared with Hargitt's description and type specimen. These were compared with Levinsen's holotype of *L. maxima* and with another specimen of *L. maxima* from Greenland.

L. maxima superficially resembles a finger sponge. It has slightly branching stems which consist of many parallel tubes from which arise the hydranths, gonangia, and nematophores. With a height of up to 15 cm and a thickness of as much as 5 mm, the stems represent an extreme example of a fascicled hydroid stem.

Dormant hydroids were collected in the summer of 1975 off Cape Cod. Hydranths and nematophores developed in the laboratory at 5-7°C.

Some specimens sent out simple stolons which anastomosed to produce a reticulum, and hydranths developed from them. This condition, I believe, imitates a stage in the early development of the species. Later the hydrorhiza becomes a complex tangle of stolons making a mat as much as 0.5 mm thick.

The site of collection, 41°37'N, is the most southern known for this northern species.

INTRODUCTION

Hargitt (1909) described as a new genus and species of hydroid, *Keratosum complexum*, from Massachusetts. Superficially, it resembled a finger sponge, rather than a hydroid. Before reaching Hargitt, the specimens had been referred to a sponge taxonomist and to a bryozoan authority. Hargitt chose the name *Keratosum* to suggest its resemblance to a sponge. His description was as complete as possible from preserved specimens which had been dormant when collected. I have been able to collect one good specimen and several poor ones from the type locality. Comparison of specimens, as detailed below, make it certain that this hydroid is the well-known northern species *Lafoeina maxima* Levinsen, 1893. By studying the growth and development of specimens I have been able to understand why descriptions vary considerably, and why there has been uncertainty in the proper systematic placement of Hargitt's *Keratosum*. More importantly, the pattern of growth which produces a massive structure quite unlike that of most hydroids can be understood; and some details can be added to what is already known only on the basis of studies of preserved specimens.

The following comments by Hargitt, Fraser, Broch, and Hirohito indicate the difficulties in determining whether Hargitt's hydroid is in fact conspecific with *Lafoeina maxima*.

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Hargitt (1909, p. 380): "In 1892 Levinsen described a hydroid from Greenland, which seemed to have much in common with the one here under review. He had described it as a new species under the genus *Lafoeina* Sars, 1873, naming it *L. maxima*. At first it was thought the present species was probably identical with it, but when one undertook to work out details of morphology it became *more or less certain* that it was not the same species, but that moreover, it could hardly belong to the same genus . . ." [Italics not in original.]

". . . it seems very sure that the present one must find different generic housing. For example, in Sars' (1873) genus the hydroid has a reticulate hydrorhiza, and Levinsen describes something of the sort for *L. maxima*, but in the present species while there may be comprised something of the sort, it would be more correct to describe the complex stem as arising from a dense sponge-like base, etc." [I wonder what else he had in mind.]

Fraser (1944, p. 173): "This species [Hargitt's] seems to have some general resemblance to *Lafoeina maxima*, but differs from it too greatly to be placed with this species, if reliance can be placed on the figures.

"Possibly because the material was obtained at such a time of the year that it was not in good condition for diagnosis, the description and figures are not definite enough to decide upon its affinities, or even to be quite sure that it is a hydroid."

In writing the above, Fraser contradicts his earlier (1927, p. 327) statement: ". . . good reasons for believing that Hargitt's specimens belong to it [*Lafoeina maxima*]."

Broch (1909, p. 165) wrote that ". . . there seems to be good reason for believing that Hargitt's specimens belong to it [*Lafoeina maxima*], although because the specimens were imperfect, some of the important features were not readily recognizable."

Our initial interest in trying to collect specimens of Hargitt's hydroid was a result of plans for a visit by Emperor Hirohito of Japan to the Woods Hole scientific community in October, 1975. He had commented on *Keratosum* as follows (Hirohito, 1967, p. 4):

"The genus *Keratosum* may be assigned to the family [Clathrozonidae] as suggested by Stechow (1923, p. 59), because in this genus, which is represented by a single species, *K. complexum* (Hargitt, 1909, p. 379), the skeleton consists of an axial part made up of more or less parallel and anastomosing stolons and a peripheral part composed chiefly of hydrothecae and nematothecae. Nevertheless, the hydranths and gonothecae were missing from all of Hargitt's materials, so that the systematic position of the genus has remained undetermined to this day. Such being the case, the status of *Keratosum* is set aside from the present discussion."

Indeed, Stechow (1923, p. 59) placed *Keratosum* in the family Clathrozonidae but added: "Systemat. Stellung unsicher!"

In a second paper, Hargitt (1911) decided that *Keratosum* belonged in the same family as *Clathrozoön wilsoni* Spencer, 1891. I mention this only to complete the record since the identity of *Keratosum* with *Lafoeina* makes Hargitt's proposal irrelevant. The family Campanulinidae, in which *Lafoeina* is placed, is distinguished from other families of thecate hydroids in having a radially symmetrical hydrotheca bearing an operculum. The operculum would not have been observable in the poor specimens which Hargitt studied.

MATERIALS AND METHODS

The specimens used are described beyond. The most useful was dredged at Crab Ledge about 9 km east of Chatham, Cape Cod, Massachusetts, 41°37.4'N,

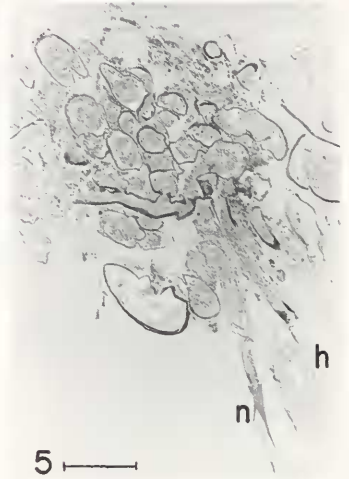
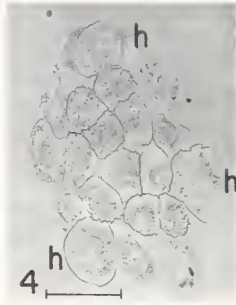
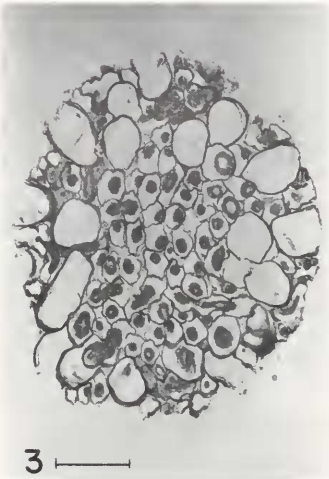


FIGURE 1. Crab Ledge 1975, specimen. Photographed soon after collection. The width of the rock at the base is 10 cm.

FIGURE 2. A part of the Crab Ledge, 1975 specimen. The height of the tallest stem is 8 cm.

FIGURE 3. Cross section of a stem of the Crab Ledge, 1975 specimen. Bar = 0.5 mm.

FIGURE 4. Cross section near the tip of one of the stems of the Holstensborg specimen. h, hydranth. Bar = 0.5 mm.

FIGURE 5. Cross section of a stem of the Holstensborg specimen. h, hydranth; n, nematophore. Bar = 0.5 mm.

69°49.1'W, 8 August 1975 (Fig. 1). Pieces of this specimen are in the Gray Museum of the Marine Biological Laboratory, Woods Hole, Massachusetts; in the collection of the Biological Laboratory, Imperial Household, Tokyo, Japan; in the United States National Museum of Natural History—Smithsonian Institution (No. 60352); and in the author's collection.

Soon after collection, many of the stems were removed from the rock; some were preserved in the next few days, others were placed in jars of sea water in a refrigerator. During transfer to Indiana University, 17–19 August, the jars were surrounded by ice, then put in a refrigerator at 5–7°C. Although the stems were

dormant when collected, some of them later developed hydranths, nematophores, and stolon outgrowths.

A good specimen was furnished through the kindness of Kay Petersen from the Zoologisk Museum, København. Data: Holstensborg, Greenland, 29 June 1908, Legit: "Tjalfe" st 88. Det. P. L. Kramp Journal 26-11-1908. Except for the Crab Ledge, 1975, specimen, this is the only one which shows developed hydranths. A small piece of it was sectioned.

I was lent a part of the holotype of Levinsen's (1893) specimen, also from the museum in Copenhagen. It was collected near Greenland. A small piece of this was sectioned and the rest returned.

J. S. Rankin gave me a specimen labeled: "Off Race Point, 190 feet [58 m], 9 July 1976, R/V Westward, 70°11'W, 42°08'N." Another specimen from Crab Ledge collected in July, 1977, was kept alive through the following fall. Although some buds developed in September none completed the formation of normal hydranths.

The National Museum of Natural History—Smithsonian Institution lent me the type of *Keratosum complexum* Hargitt "No. 42232, Crab Ledge, Mass. Sta 7835, 18 fms [32 m], by 'Fish Hawk' and R. C. Osburn on 2 September 1903 and 23 July 1907." It is presumed that Hargitt lumped the collections from both dates together. [The 1907 collection must have been at Station 7835, and 1903 collection at one of the stations 7603–7609 (Summer *et al.*, 1911, part 1, p. 203–204.)]

Specimens were fixed using Bouins followed by 70% ethanol. Routine paraffin methods were used for sectioning, followed by hematoxylin and eosin stains. The specimen used for the scanning electron micrographs was anesthetized using magnesium sulfate, fixed with gluteraldehyde, further fixed with osmium tetroxide, and coated with gold palladium.

MORPHOLOGY

Stems and basal mat

My best specimen (Fig. 1) from Crab Ledge, 1975, was on the upper surface of a rock. The rock surface was completely covered by a dense mat about 0.5 mm thick. The mat or hydrorhiza consisted of a tangle of stolons and, as viewed from above, of openings of hydrothecae similar to those on the surface of the stems. There were more than 100 upright stems, some with a few branches which bent upward. Pieces removed from the rock (Fig. 2) resemble Hargitt's figure. The Holstensborg specimen has the same colony form. The tallest stems are 10 cm high, the thickest have a diameter of 3 mm at their bases. Shorter stems have diameters of 1–2 mm. Each stem tapers to a rounded tip. The color is a light tan near the tips and darker toward the bases. The surface of the stems seem fairly smooth since the hydrothecae and nematothecae had been worn down to a common level (Fig. 3). The stems feel spongy.

The specimen provided by Dr. Rankin consists of a shell of *Spisula*, 11 cm broad, on which are scattered about 40 stems. Several of the stems are in clumps with a common hydrorhiza, while other arise singly. Their height varies from 0.7 to 4 cm with an average of about 1.5 cm.

One of the Holstensborg specimens consists of a mat from which three stems arise. The length of the longest is 7.5 cm and at its thickest has a diameter of 5 mm. It seems to have been taken from a ribbed shell since there are grooves on the underside of the mat. Because this specimen had well-developed hydranths and

nematophores its surface appears more shaggy than any of the others. The other Holstensborg specimen consists of a mat with four stems which are shorter and thinner than those of the larger specimen.

Stems from both Levinsen's (1893) and Hargitt's (1909) types resemble my specimens from Crab Ledge. The Crab Ledge, 1977 specimen is different only in that the tallest stem is 15 cm high, a value which is the extreme cited by Naumov (1969, p. 340) for the species.

Each stem consists of a central axis of parallel tubes. Each tube is like a stolon or hydrocaulus in consisting of an outer perisarc and an inner coenosarc enclosing a gastrovascular cavity.

The stems of most tall hydroids consist of several adherent hydrocauli and are said to be fascicled. *L. maxima* may be regarded as an extreme example of a fascicled hydroid stem.

The cortex of a stem consists of hydrothecae, nematothecae, and gonothecae. In addition, as more tubes develop they must occupy the spaces between the thecae which had developed earlier.

In a young stage when there are only a few tubes, the thecae extend freely from the stem as figured by Naumov (1969, p. 340) and by Fraser (1944, Plate 31, Fig. 146). Figure 4 is a section close to the tip of a stem of the Holstensborg specimen. Here there seem to be 14 tubes and three or four hydranths, one of which, at the tip of the section, is connected with a tube. Figure 5 shows an intermediate condition of a thicker stem of the Holstensborg specimen. Figure 3 is of a dormant stem from a Crab Ledge, 1975, specimen. The distal portions of the hydrothecae and nematothecae have been eroded but the proximal portions are rather deeply imbedded in the stem and the cortical region has a large number of tubes. In Figures 7 and 8 of a living specimen, only the most distal one third or one fourth of the hydrothecae extend beyond the surface of the stem.

Hydranths and hydrothecae

The hydranths arise directly from the tubes. The hydrothecae are slightly narrower proximally and, as noted above, they may be free or imbedded through most of their length in the cortex of the stems. Naumov (1969) reports their height as 0.8–1.4 mm.

In the sections of Levinsen's type a few hydrothecae extend beyond the general surface of the stem and the longest measured is only 0.6 mm. Its real length cannot be determined since it may be partly eroded distally and its connection to its tube is missing in the sections. The sections of the Holstensborg specimen show a few hydranths whose hydratheca are 1.1 mm long. As with the Levinsen sections, none of mine show the full length of a hydrotheca; the longest measurement was 0.5 mm but the free region of the theca was wrinkled and the proximal region not in the section. An estimate of 0.8–1.0 seems reasonable.

The diameters of hydrothecae measured near the distal end have a range from 136–238 μm . Averages for Levinsen's: 140 μm ; Holstensborg: 214 μm ; Crab Ledge, 1975: 195 μm . I suspect that the lower value from the Levinsen sections may be because the material (after nearly 90 years) is somewhat shrunken. The slight difference between the Crab Ledge, 1975, and Holstensborg specimens is possibly real. Figure 7 shows several hydrothecae in profile and the variation in diameter can be seen, as well as variation in the angle with respect to the axis of the stem. Naumov reports that the hydrothecae are at an angle of 45–60° with the mouth toward the apex of the stem. Fraser's figure shows this feature as does Hargitt's.

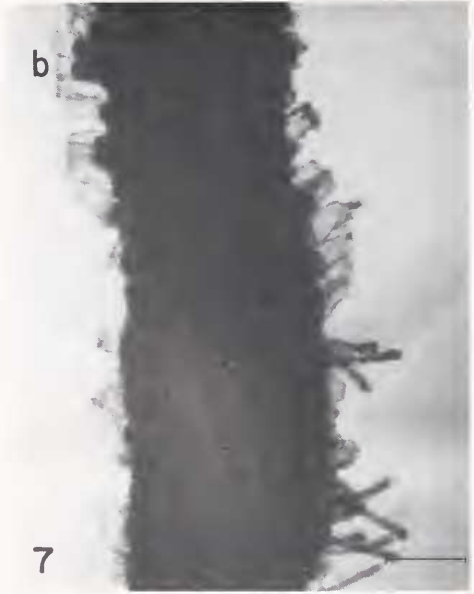


FIGURE 6. New growth of hydrocauli from the tip of a stem. 24 Sept. 1975. b, young hydranth buds. Bar = 0.5 mm.

FIGURE 7. Same stem as in Figure 6 with same hydranth buds and clusters of nematophores. Bar = 0.5 mm.

FIGURE 8. Hydranths, 20 Nov. 1975. Bar = 1 mm.

Near the tip of some of our active stems this feature is also seen, but in the more proximal regions of older and thicker stems, the hydranths and hydrothecae are nearly at right angles to the stem as shown in Figures 7 and 8.

Operculum

The operculum consists of about 12 triangular plates or lappets which project outward from the circular opening of the hydrotheca. When first formed the plates are continuous with the wall of the hydrotheca. Only after they have folded is a definite base established. While the opercular plates are nearly equally long for each hydrotheca, they show considerable variation at their bases. One hydrotheca, for example, had plates whose bases varied in width from 26 to 53 μm . The length of measured plates ran from 170 to 205 μm . When the hydranth is not extended the plates meet at their tips to form a cone slightly taller than its base. They open when the hydranth is extended. Often, in empty hydrothecae, the plates have collapsed inward. Many hydrothecae lack the plates, but these are cases in which the hydranth itself has regressed. In poor specimens most hydrothecae have been worn or broken so that they do not project beyond the surface of the stem as in Figure 3.

The body of the hydranths can extend more than a millimeter beyond the hydrotheca (Fig. 8). The longest measured from mouth of a hydrotheca to base of tentacles was 1.4 mm. The extended tentacles are nearly 0.5 mm long. In the SEM picture (Fig. 9), both the tentacles and body are partly contracted.

Tentacles

The hydranths of our specimens had 12 tentacles. Although our records show a few counts of 11 or 13 this is likely due to the difficulty of observation since thecate hydroids as a rule have an even number of tentacles as shown by Berrill (1949). One of the sections of the Holstensborg specimen had been cut across the tentacles and an exact count of 16 was possible. Counts of tentacles of hydranths on the stems gave values close to 16. The difference between 12 and 16 may reflect a more favorable environment for development in the Holstensborg specimens. In



FIGURE 9. SEM showing two partly contracted hydranths. 24 Nov. 1975. Bar = 200 μm .
 FIGURE 10. Stolons growing out from the basal disk. 20 Nov. 1975. Bar = 1 mm.

hydroids the number of tentacles in a species shows some variation so no systematic distinction should be made on the basis of small variations in tentacle number. For example, hydranths of *Clathrozoön wilsoni* have 12–16 tentacles (Hirohito, 1967), and the sketch of his Plate IV shows this variation among hydranths of the same stem.

Gonangia

I have found gonangia only in a few of the sections of the Holstensborg specimen. The diameter of the gonotheca is slightly more than 300 μm . The tissue is not satisfactory for critical examination. I can add nothing to Broch's (1909) statement: "In the gonotheca of the studied individuals there are several planula larvae, but the fixed material gave no detailed understanding of the gonangial condition." [My translation.]

Nematophores

These extend above the surface of the stem by about 750 μm . The nematophores of Naumov's (1969, p. 340) figure are about 700 μm long. Their thickness is slightly less than 100 μm , and they may or may not show slight enlargement at the tip. The nematocysts conform to the type called basitrichous isorhizas by Weill (1934). The capsules are from 14 to 20 μm long and about 4 μm wide. A few were successfully discharged. Measurements of the barbed region were 14–18 μm , and the longest thread 160 μm . The nematocysts are closely packed in the tip of the nematophore. In sections of two nematophores, I was able to count 48 in six successive sections, 38 in four successive sections, the actual number must be more than 50.

DEVELOPMENT

Following their collection on 8 August 1975, stems were removed from the rock, placed in separate glass jars which were kept in refrigerators except during transportation when they were surrounded by ice water. Some stems were at first kept in a cold room at 16–17°C, but by 16 September all were kept refrigerated at 5–7°C.

The photograph (Fig. 6) taken 24 September shows new growth of the tubes which constitute the central core of stems. Hydranth buds had appeared by this time, and the same two buds are seen in profile in Figures 6 and 7. Also, several nematophores had developed as shown in Figure 7. In the following days many more buds were produced. Some of these developed tentacles, but none emerged from the hydrothecae as fully developed normal hydranths. Whether tentacled or not, these buds regressed leaving empty hydrothecae, a few of which are shown in profile in Figures 6 and 7.

Some, but not all, of the stems produced normal hydranths. On 21 November normal hydranths were observed on one stem, and it and two other stems of the same specimen had normal hydranths through 12 December; after that date, no observations were made until 29 December. The records show no fully developed hydranths on 29 December nor during the next week; finally, however, there was a new burst of hydranth development which ran from 9 January through 13 January. After that time buds were observed but no fully developed hydranths.

Another specimen produced complete hydranths from 18 November to 24 November. Figure 8 shows some of the hydranths of this specimen on 20 November.

It again produced feeding hydranths from 29 December through 10 January. Thereafter, buds were produced which did not complete development.

Four other specimens produced normal hydranths during only one period. The dates are: 1–14 January; 6 January–10 February; 29 December–15 January; and 29 December–2 January.

I made only a few observations to determine the length of life of individual hydranths. Of four hydranths identified on 9 January, only one remained five days later. The others had regressed; that is, they had not merely withdrawn. While this regression was taking place, young buds were appearing nearby. In the few cases which have been studied closely, hydranths of thecate hydroids have been shown to regress after about a week; and frequently after a few days another hydranth is produced at the same location. An earlier paper (Crowell, 1953) on regression and replacement cites other investigations of this problem.

The basal mat or hydrorhiza consists of a mass of tangled stolons. Single stolons grew out from this in several of our animals (Fig. 10) and in one case attached to the side of the jar. Here they were not easily observed, but at the time when specimens were preserved, the jar was broken and the stolons could be examined as well as the hydrothecae which had arisen from them. It is clear that stolons often fuse so that the hydrorhiza is a true reticulum. Most of the stolons lack coenosarc in the preserved specimen. Most hydrothecae are empty and only a few undamaged. When a new colony of *L. maxima* is established, it must at first take this form. At that time it might easily be mistaken for *Lafoeina tenuis* Sars, 1873.

Levinsen distinguished *L. maxima* with its thick mat from *L. tenuis* with its simple reticulate stolon system. As indicated above, this distinction would not apply to young specimens. Levinsen points out that there are only 4–6 large nematocysts at the tip of each nematophore in *L. tenuis* while there is a large, rounded battery of very small nematocysts in the nematophore of *L. maxima*. While I obtained counts of nearly 50 nematocysts for nematophores of *L. maxima*, Sars' figures show only a few, and these are represented as twice the size of those that I measured. The tips of the nematophores of *L. tenuis* are conspicuously swollen, only slightly or not at all in *L. maxima*.

DISTRIBUTION

Naumov (1960, 1969, p. 340) says: "All Russian northern and Far Eastern Seas, Davis Strait, Norwegian and Greenland seas. In Sea of Japan occurring at threshold depths for this species." Vul'fius (1937, p. 72), in translation, says: "Bay of Peter the Great, 1600–900 m; south of the Rimskogo-Korsakova Islands, 410–366." A chart shows that the edge of the continental shelf south of the Bay and Islands is at about 42°25'N. At 42°10'N the depths are more than 1600 m. Therefore, for the western Pacific the most southern report at about 42°20'N is slightly farther north than Crab Ledge at 41°37'. In addition to our localities, there are two in the Gulf of St. Lawrence (Fraser, 1944), and several in northern Canada (Calder, 1970). I know of no records for the eastern Pacific.

Colton and Stoddard (1973) furnish tables of bottom temperatures. For the Crab Ledge location, maximum temperatures in January through April range from 2.9°C to 5.0°C, and maxima in June through November 8.2°C to 12.6°C. I agree with Hargitt's conjecture that the elevated summer and fall temperatures are responsible for the dormant condition of specimens collected in those seasons.

ACKNOWLEDGMENTS

I have received assistance from so many people that it is impractical to name them all. Included would be the paid and the volunteer crew of the "expedition" of August, 1975, authorized by the Director of the MBL; members of the Gray Museum who provided facilities for handling the specimens; those who furnished other specimens; translators of Latin, Norwegian, Danish, and Russian; and several critics of the manuscript.

Several colleagues took the photographs for the figures: Fig. 1, Charles Wyttenbach; Fig. 2, Ray Ritz; Figs. 3, 4, & 5, David Dilcher and Carl Longstreth; Figs. 6, 7, 8, & 10, George Malacinski; and Fig. 9, Rudolph Turner.

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